Can ocean acidification affect population dynamics of the barnacle *Semibalanus balanoides* at its southern range edge?

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Abstract. The global ocean and atmosphere are warming. There is increasing evidence suggesting that, in addition to other environmental factors, climate change is affecting species distributions and local population dynamics. Additionally, as a consequence of the growing levels of atmospheric carbon dioxide (CO_2), the oceans are taking up increasing amounts of this CO_2, causing ocean pH to decrease (ocean acidification). The relative impacts of ocean acidification on population dynamics have yet to be investigated, despite many studies indicating that there will be at least a sublethal impact on many marine organisms, particularly key calcifying organisms. Using empirical data, we forced a barnacle (*Semibalanus balanoides*) population model to investigate the relative influence of sea surface temperature (SST) and ocean acidification on a population nearing the southern limit of its geographic distribution. Hindcast models were compared to observational data from Cellar Beach (southwestern United Kingdom). Results indicate that a declining pH trend (-0.0017 unit/yr), indicative of ocean acidification over the past 50 years, does not cause an observable impact on the population abundance relative to changes caused by fluctuations in temperature. Below the critical temperature (here $T_{crit} = 13.1°C$), pH has a more significant affect on population dynamics at this southern range edge. However, above this value, SST has the overriding influence. At lower SST, a decrease in pH (according to the National Bureau of Standards, pH_{NBS}) from 8.2 to 7.8 can significantly decrease the population abundance. The lethal impacts of ocean acidification observed in experiments on early life stages reduce cumulative survival by ~25%, which again will significantly alter the population level at this southern limit. Furthermore, forecast predictions from this model suggest that combined acidification and warming cause this local population to die out 10 years earlier than would occur if there was only global warming and no concomitant decrease in pH.

Key words: barnacle; biogeography; climate change; ocean acidification; population model; Semibalanus balanoides; southwestern United Kingdom.

INTRODUCTION

Models are useful tools for exploring the relationships between environmental factors (biotic and abiotic) and population dynamics (Lauzon-Guay et al. 2006). In the study of the marine environment, models have been used to understand processes such as local and regional-scale population dynamics (Lima et al. 2007, Wethey and Woodin 2008), dispersal (Wieters et al. 2008), and interspecific interactions (Poloczanska et al. 2008). The majority of these models assume temperature to be the dominant controlling factor. Increasing atmospheric CO_2 is enhancing the greenhouse effect causing atmospheric and ocean warming. Certainly, as climate change research progresses, it is becoming increasingly important to understand the role temperature plays on

population processes, how this role changes across both temporal and spatial scales, and whether we can make useful predictions. Climate change is not, however, the only consequence of elevated atmospheric CO_2 concentrations. The oceans are a carbon sink and have absorbed ~48% of all the anthropogenic carbon released into the atmosphere since the industrial revolution (Sabine et al. 2004). This increasing concentration of CO_2 in the ocean is altering the ocean chemistry, predominantly causing an increase in hydrogen ions (and hence a decrease in pH) and a decrease in carbonate ions (Orr et al. 2005). Ocean acidification, as it has been termed, has seldom been included in biological models. Only one paper to date has investigated ecological dynamics and their correlation to pH dynamics over the same time period (Wootten et al. 2008).

Wootton et al. (2008) provided observational and modeling analysis of rocky-shore community dynamics in relation to pH and associated physical factors over nine years (2000–2008). Their analysis records that there

has been a decrease in ocean pH over this period of 0.045 unit/yr, which is significantly faster than seen in other long-term time series station data, such as the Hawaiian Ocean Time-series (HOT; Dore et al. 2009), the European Station for Time Series in the Ocean, Canary Islands (ESTOC; Santana-Casiano et al. 2007), and the Bermuda Atlantic time series (Bates 2007). Associated with the declining pH shown by Wootton et al. (2008) is a shift in ecosystem structure from a mussel to an algal–barnacle-dominated community. Ocean acidification can alter processes such as calcification (e.g., Gazeau et al. 2007), growth (e.g., Michaelidis et al. 2005), immune function (Bibby et al. 2008), and behavior (Bibby et al. 2007). However, understanding how these individual impacts acting together alter behavior and interactions between individuals, populations, and communities is more difficult.

Barnacles are among the best studied of intertidal animals, and available literature (e.g., Barnes 1999) indicates that their population dynamics can be influenced by many factors. It has long been debated whether pre-settlement or post-settlement factors contribute more to controlling recruitment of barnacles (Hatton and Fischer-Pietter 1932, Hatton 1938). Field observations and dispersal models suggest that pre-settlement conditions play an important role, e.g., wind strength and pattern during the larval phase (Kendall et al. 1982, Delafontaine and Flemming 1989). However, survival of settled post-larvae and juveniles has been shown to be highly influenced by temperature over the summer months (Kendall et al. 1985) as well as by predation and abrasion (Connell 1961, Foster 1971). Thermal models have been developed to show that the temperature on a rocky shore can exceed barnacles' thermal limits and their survival depends on small-scale habitat conditions such as position on the shore (Wethey 2002). Poloczanska et al. (2008) developed an environmentally driven population model, which uses sea surface temperature (SST) to force recruitment. This model successfully predicts the population dynamics of two interacting barnacle species and was used to investigate the response of these two competing species to climate change (Poloczanska et al. 2008). Few modeling studies attempt to include multiple factors for forcing the population, despite the multitude of factors occurring in the oceans, which taken together have the potential to substantially alter ecosystem dynamics (Helmuth et al. 2006). There is also a need to take empirical evidence of impacts on single organisms, even at the level of cellular and physiological processes, and place this in a wider context of how these impacts might affect a population or even a community. Additionally this provides an opportunity to assess how a population responds to the narrowing of a species thermal window by the addition of a stress such as declining pH (Pörtner and Farrell 2008).

The purpose of this present study was twofold: (1) to incorporate the impacts of ocean acidification into a population model forced through environmental parameters and (2) to scale up from experimental data to predict how populations might be impacted by ocean acidification and climate change. This is the first study, to the authors' knowledge, that attempts to place ocean acidification experimental data into a population model for a benthic sessile organism. We have adapted a model used to predict climate change impacts on two barnacle species (Poloczanska et al. 2008). We used this modified model to predict yearly changes in S. balanoides populations using experimentally determined data on survival of post-larvae under different ocean acidification and climate change scenarios and compared these with data from the southwest coast of England. We then used the model to (1) hindcast and forecast the population abundance at the southern edge of the S. balanoides geographic distribution and (2) to quantify the relative sensitivity of this species to ocean acidification and climate change.

METHODS

Data sets

Population data.—Semibalanus balanoides abundance data were extracted from Southward (1991: Table 1) as the mean adult abundance (measured as the number of individuals per square centimeter) at all tidal heights from autumn 1951 to 1990. The counts were made at Cellar Beach (50°18′ N, 004°3′ W), on the south coast of England. Autumn counts are used here because they give a good indication of the population after the spring/summer recruitment period and survival of recruits over the summer including that year's settlement.

Sea surface temperature (SST) data.—The SST data were obtained from station E1 (Western Channel Observatory; available online)[5] from 1903 to the present (2008). The data for June SST were used following Poloczanska et al. (2008), in which June SST from the previous year emerged as the best predictor for the model (Fig. 1a). The variation around the data was calculated ($\sigma^2 = 1.17$), as was the linear trend (June SST $= 0.0142 \times$ year $- 13.799$, mean square deviation [MSD] $= 0.9786$).

Future projections were based on the following scenario: T1, extension of the linear trend observed in the E1 SST data from 1903 to 2008 (+0.0142°C/yr), with stochastic variation added to the mean linear trend (Fig. 1b) to match the variance observed in the E1 data ($\sigma^2 = 1.17$).

pH data.—pH data were available for this location but only for one time point. One pH data set was created in 1922 (Atkin 1923) at several locations off Plymouth Sound, including at station E1 (June pH = 8.23). The nearest long-term time series of pH is the ESTOC, data from which have been used to show that pH is decreasing by 0.0017 unit/yr (Santana-Casiano et al.
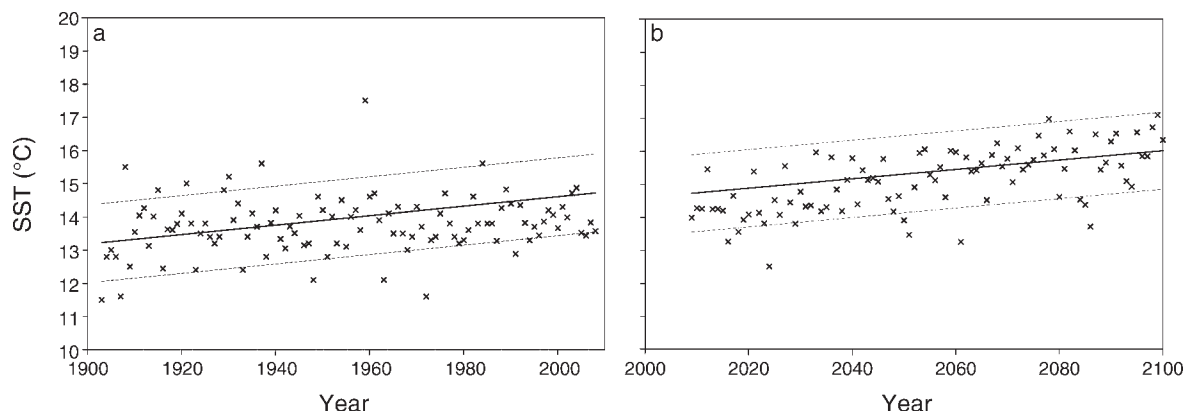
Fig. 1. (a) Temperature data set used in the model for the 1903–2008 period off Plymouth, UK. The mean temperature (black line) is increasing by 0.0142°C/yr, and dashed lines indicate ±SD ($\sigma^2 = 1.17$). Crosses show the Western Channel Observatory (station E1), Plymouth, UK, data set for temperature. (b) Future projection: modeled temperature with mean increase 0.0142°C/yr (black line) with associated example of stochastic data set (black crosses); dashed lines indicate ±SD ($\sigma^2 = 1.17$).

2007). From this information we modeled pH for the same period as available temperature data (1903–2008) as a linear pH decline (Appendix C: Fig. C1) with stochastic variation added by calculating the variation found in the available Waterbase database June pH data (Applezak 30-km station, 1975–1982, which is a similar distance to E1, 34 km offshore; $\sigma^2 = 0.119$; Fig. 2a; Netherlands Ministry of Transport, Public Works, and Water Management, *available online*).[6]

Additional pH data were collected from the rocky intertidal over two tidal cycles (over 13 hours) at Cellar Beach in June 2009 (Fig. 2a and Appendix C: Fig. C2); measurements were made at the sea surface 50 cm out from the waterline (for most of the tidal cycle these were above the rocky shore); however, at low tide measurements were made over the sandy bottom (marked with an asterisk on Appendix C: Fig. C2) and are not representative of the water chemistry that a rocky-shore barnacle would experience.

Future projections were based on the following scenario: pH1, extension of the linear trend described in the ESTOC data (−0.0017 pH unit/yr) with stochastic variation added to the mean linear trend (Fig. 2b) to match the variance in the pH data set ($\sigma^2 = 0.119$).

Model description

The model was based on that of Poloczanska et al. (2008) but was modified to model only six *Semibalanus balanoides* age classes. The basic assumptions were: (1) the population is open and recruitment is proportional to the free space available; (2) mortality is age-specific and density independent; and (3) that *Chthamalus–Semibalanus* interactions were not important at this site, as the two species are not in full competition for space since there is always some free space for settlement (Southward 1991). The model has two time steps per

year (June and December), with *S. balanoides* recruiting to the adult population in June. The number of individuals entering each age class of six months and above is calculated as

$$n_{i+1,t+1} = p_i n_{i,t} \qquad (1)$$

where p_i is the probability of surviving the six months from age class i to age $i + 1$ for species x. The last age class was assumed to be additive. The input parameters, survival size, growth rates, and maximum recruitment values, are taken from Poloczanska et al. (2008) (Appendix B: Table B1).

Recruitment, R, is defined as the number of settlers alive at the end of the settlement season, taken to be June for *S. balanoides* as in Poloczanska et al. (2008). The equations are provided in Appendix B: Table B2.

Recruitment rate, S, is an SST- and pH-dependent function (Fig. 3):

$$S_t = S_{max} \times f(\text{SST}, T_{crit}, c) \times A_{pH} \qquad (2)$$

where S_{max} is the maximum recruitment rate per unit free space at cool temperatures, set to a constant 30 recruits per square centimeter; f is a cumulative Gaussian function; SST is June SST; T_{crit} is the SST at which recruitment is at 50% maximum (in the SST-only model, T_{crit} is constant [$T_{crit} = 13.11$]; in the pH and SST combination model, T_{crit} is a function of pH [$T_{crit} = 1.4029\text{pH} + 1.6023$] with the model fit to the data from experiments); c represents the rate of decline of recruitment per unit free space with increasing SST. A_{pH} is the interaction of pH and temperature on survival such that when the SST-only model is used, $A_{pH} = 1$, and when the pH and SST combination model is used, A_{pH} is a function of pH:

$$A_{pH} = (0.554\text{pH}^2 - 8.643\text{pH} + 34.593) \qquad (3)$$

for $7.7 \leq \text{pH} \leq 8.2$). The interaction of SST and pH was parameterized from experimental data on the probabil-
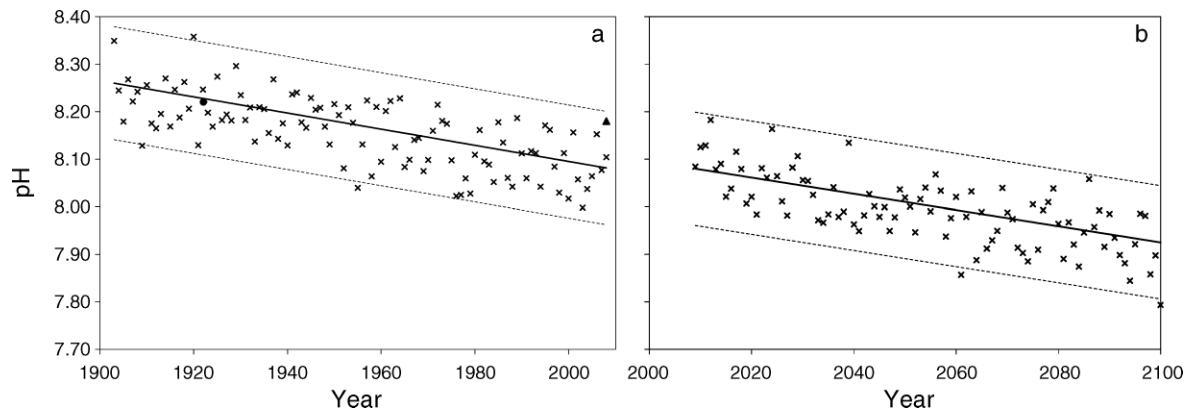
Fig. 2. (a) Example of modeled pH data set for the 1903–2008 period. The solid line indicates mean pH $= -0.0017$ unit/yr $+ 11.498$, the dashed lines indicate $\pm$SD ($\sigma^2 = 0.119$), the crosses are an example of the random distribution of pH values selected for one data set, the solid circle represents data from Atkins (1923), and the solid triangle represents data from Cellar Beach, June 2008. (b) Modeled future projection: pH1 with mean decrease of 0.0017 unit/yr (solid line) with associated example of stochastic data set (crosses).

ity of recruits surviving at each SST and pH (Findlay et al. 2010). pH and SST produce a response in recruitment similar to the function of aerobic scope hypothesized by Pörtner and Farrell (2008).

Statistical analysis

The model runs were compared to the Southward (1991) data (from 1950–1990) by calculating the sum of squared deviation (SS^2), the Pearson's correlation coefficient (r), and the Akaike's information criterion (AIC). An $SS^2 = 0$ or $AIC \leq 0$ shows a model that does not deviate from the data (i.e., good fit and position), while an $r = 1$ would demonstrate complete correlation between model and data (i.e., good phasing and cycling).

To assess the differences between the data and the model hindcast runs (1950–1990), the SS^2 and r were compared with the average (mean of 100 runs) SS^2 and r for the time series with decreasing pH (-0.0017 unit/yr) by converting both to z values. It was assumed that the 100 runs came from a normal distribution and that the z value standardizes the normal.

Experimental analyses

We also used empirical evidence to infer whether, over the whole life cycle of Semibalanus balanoides, it is possible to achieve the levels of mortality in lowered pH conditions that will cause a significant impact on the population. For this we use experimental data on survival of embryos (Findlay et al. 2009a), nauplius
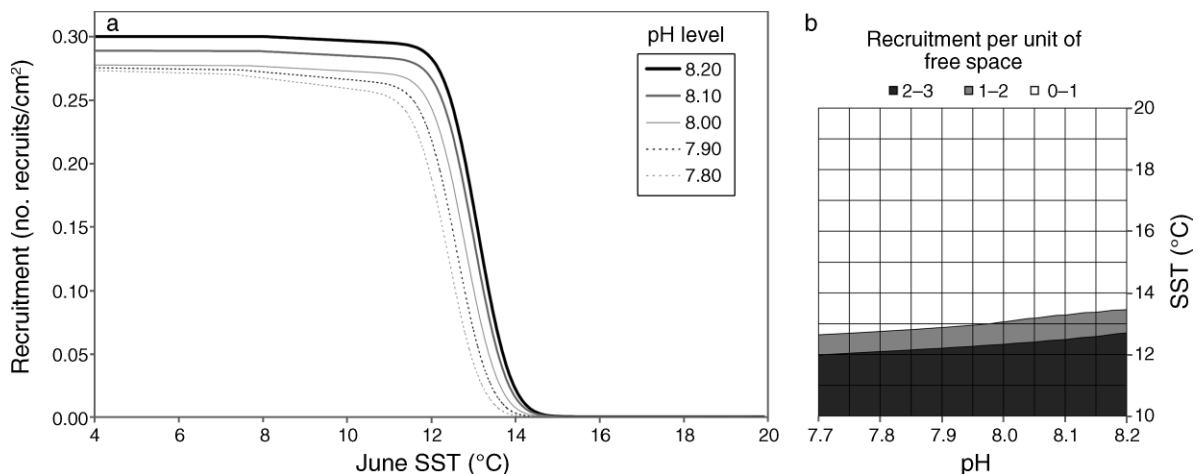

Fig. 3. (a) Fitted function for recruitment rate of the acorn barnacle Semibalanus balanoides per unit free space with June sea surface temperature (SST) and at different pH levels. (b) Recruitment rate per unit free space is illustrated as a function of June SST and pH.

larvae (detailed in Appendix A), and post-larvae (Findlay et al. 2009b).

Results

Model comparison to Semibalanus balanoides abundance data 1950–1990

The model (SST only forcing) is able to reproduce the Cellar Beach mean population data ($SS^2 = 47.55$, $r = 0.51$, AIC $= 17.72$; Fig. 4a). When the pH function was introduced, with the exceptions of pH $= 8.1$ and pH $= 8.0$, as the constant pH was decreased, the correlation between the data and the model also decreased (Fig. 4b; Appendix D: Table D1). pH $= 8.1$ and 8.0 had lower SS^2 deviation and AIC but lower Pearson's correlation (for pH $= 8.1$, $SS^2 = 42.27$, $r = 0.49$, AIC $= 13.14$; for pH $= 8.0$, $SS^2 = 45.27$, $r = 0.45$, AIC $= 15.81$), which suggests that at these pH levels the model prediction was better related to the data but did not accurately describe the cycling of the data. When the model of pH decreasing with time (-0.0017 unit/yr) was used, the time series produced the best combination of high Pearson's correlation and low AIC value and SS^2 deviation values in relation to the Southward (1991) data ($SS^2 = 43.10$, $r = 0.49$, AIC $= 13.90$).

Model projections for 1990–2008

The E1 SST data and decreasing pH (-0.017 unit/yr) produced a time series in which overall the abundance of *S. balanoides* had a decreasing trend. There was a large increase in 1992 when there was a below-average cold year the previous year (12.9°C) and population levels remained relatively high between 1995 and 1997. The population increased again in 2001 after a cold year in 2000 (13.7°C), although this was a much smaller increase than in 1992 because SST was warmer. After the year 2000 the population abundance decreased to near zero (Fig. 5) but appeared to recover slightly after 2005 because of a colder year in 2005 (13.7°C). There was very little difference between the time series predicted by SST only and the time series predicted by SST and pH (SS^2 deviation from temperature-only model $= 2.66$). However, at constant pH levels below 8.0, the population remained relatively low, even after the cold years of 1992 and 2001, because recruitment levels were much lower than pre-1990 levels.

Model projections for 2008–2100

After 2008, the population abundance, using SST and pH forcing, reached a maximum of ~1.5 individual/cm² (Fig. 6) but on average was <1.0 individual/cm² (mean of 100 model runs). A small increase in abundance could occur by introducing a low SST year; however, even with SST-only forcing, the average abundance was 1.5 individuals/cm². After the year 2050 and 2060 for the pH and SST forcing and the SST-only forcing, respectively, the model population died out completely. The pH and SST forcing scenario caused the population to die out

more quickly than when there was no pH function included.

Experimental survival rates

In a controlled laboratory exposure experiment (Findlay et al. 2008), *S. balanoides* embryos showed no mortality effects at 2008 southern-range winter SST (~10°C). In a subsequent experiment, nauplii began to show increased mortality in lower pH conditions after 12 days (at spring SST of ~12°C). Overall nauplii mortality increased further through days 15, 20, and 26 such that survival was 15% lower than the control after 26 days. Findlay et al. (2010) noted that the post-larval mortality varied with SST and pH, such that at low SST (4–8°C) there was negligible impact on post-larval survival (2–3% lower than the control), whereas at higher SST (14–19°C) and low pH there was more impact on survival (10–27% lower than the control). Cumulatively, these three studies have demonstrated that lowered pH decreases the survival of early life stages in the laboratory from ~79% (control) to ~58% at current summer SST (14°C). The modeled equilibrium population at 14°C (no pH affect included) is 0.803 (individuals/cm²). The equilibrium population decreases to 0.645 individuals/cm² and 0.479 individuals/cm² when a lowered survival of 79% and 58% are incorporated into the model, respectively.

Discussion

This study integrates results from an ocean acidification and climate change experiment with a population model forced by temperature and pH. It predicts how climate change and ocean acidification together might impact upon a population of the barnacle *Semibalanus balanoides* at the southern edge of its geographic range. Although sea surface temperature (SST) is the main driver in the population dynamics at this site, small decreases in pH can have a significant impact on population abundance by further lowering recruitment. Nevertheless, the projected decline in modeled pH over the past 50 years does not appear to significantly impact the population dynamics compared to the relative increase in SST over this period. Future projection for decreasing pH and increasing SST suggests that the additional contribution of pH will cause the population to die out at this location 10 years earlier than predicted with only SST increasing.

There is good agreement between the SST-only population model and the population data from Southward (1991). As with Poloczanska et al. (2008) June SST in this model is a proxy for a suite of environmental influences on the success of early life stages. Adding an additional factor, such as pH, may not result in a large change in the population dynamics as the impacts resulting from this factor may already be captured by the June SST function. Indeed, pH covaries with SST (Sarmiento and Gruber 2006). pH may have had most influence on the early life stages prior to
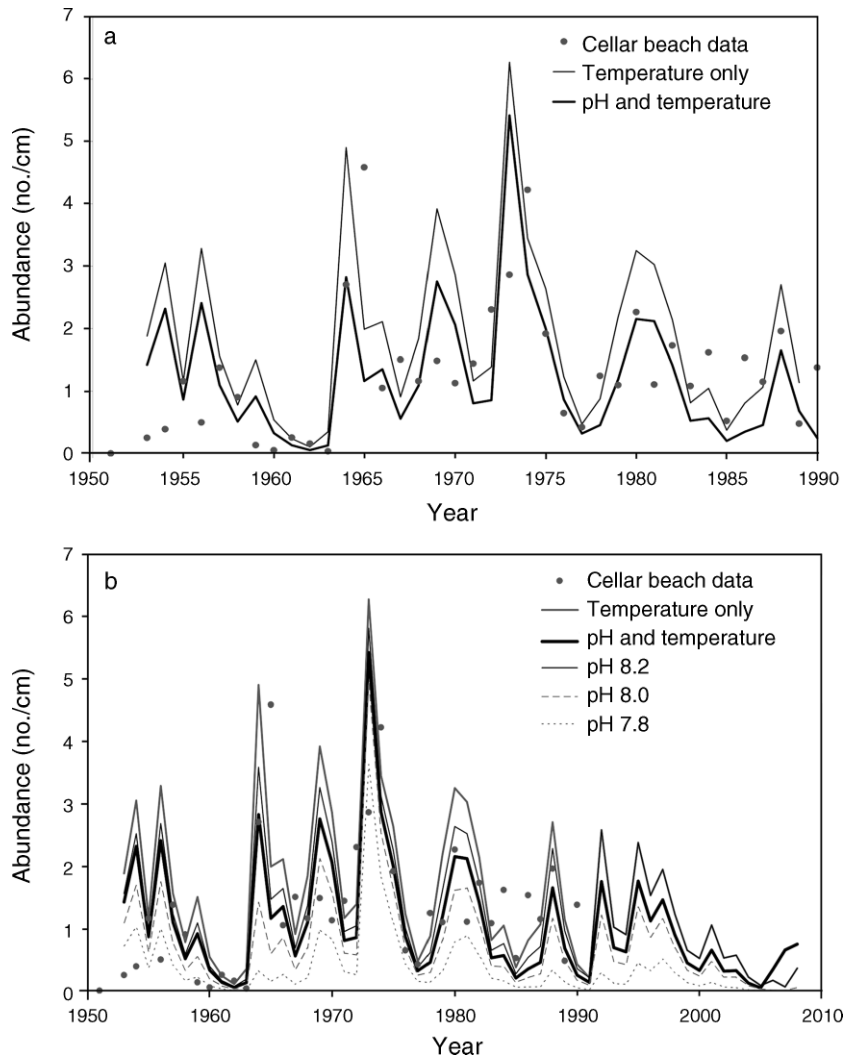
FIG. 4. (a) Temperature-only model, pH and temperature model, and data for population density of the acorn barnacle *Semibalanus balanoides* at Cellar Beach, UK (Southward 1991) between 1950 and 1990. (b) Modeled population with temperature only, temperature and decreasing pH by 0.0017 unit/yr ("pH and Temp"), constant pH = 8.2, pH = 8.0, and pH = 7.8. Circles are data from Southward (1991).

recruitment, which could either affect fitness or alter the number of settling cyprids. Pre-settlement impacts that alter fitness, such as lowered pH or altered food supply, are therefore not distinguishable in this model. The model sensitivity analysis (Fig. 7) suggests that in response to a relative increase or decrease in pH or June SST (by ±2.5%) *S. balanoides* abundance is more sensitive to changes in pH than changes in June SST up until the critical temperature of ~13°C (although these changes are nonlinear). This implies that changes in pH have more of an impact on the southern-edge populations during cold-water events in June, whereas when there are warm-water events the population responds more strongly to changes in SST.

At the southern edge of *S. balanoides*' range, increasing SST undoubtedly will result in local population extinctions as has already been observed in some

locations (Southward et al. 1995, Mieszkowska et al. 2006). Decreasing pH could potentially bring forward the time when extinction occurs and may also lead to extinctions in other areas, e.g., local upwelling, where pH is particularly low. At current June SST (~14°C) the impacts of experimentally lowered pH on survival across all the early life stages of *S. balanoides* (embryo, nauplii, and cyprids) can result in a significant reduction in population abundance.

In contrast with the predictions provided here, a community modeling study by Wootton et al. (2008) suggests that acorn barnacle abundance increased with decreasing pH over an eight-year period. Although the ecosystem investigated by Wootton et al. (2008) may be slightly different from the one at the location of this present study, it will contain similar functional groups (barnacles, mussels, fucoids, etc). It is important to
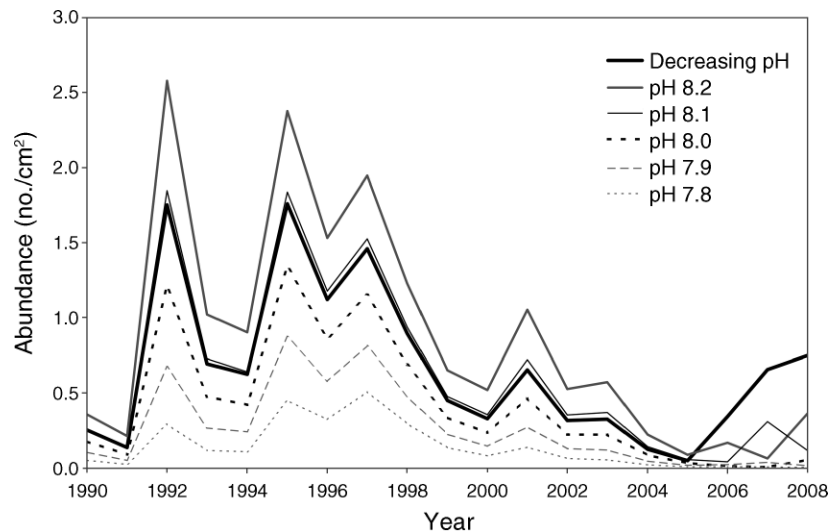
Fig. 5. A modeled acorn barnacle population from 1990 to 2008 with pH decreasing by 0.0017 unit/yr and five levels of constant pH.

compare potential difference in predictions in order to assess whether information on individuals and populations can be generalized to functional groups. The different prediction in Wootton et al. (2008) may be a response to alterations in ecosystem dynamics as opposed to a direct response to changing environmental conditions. Mussel cover on the shore appears to have decreased, giving rise to an increase in the algal–barnacle community (Wootton et al. 2008). There have been many studies investigating the patch dynamics on rocky shores, particularly with respect to space occupation and succession between limpet–fucoid–barnacle-dominated systems and mussels-dominated systems (e.g., Burrows and Hawkins 1998, Enderlein and Wahl 2004). Al-though the shift in community structure could have resulted from a decrease in pH, experimental results suggest that mussels may not be significantly impacted until much lower pH levels than those recorded by Wootten et al. (2008) (e.g., Gazeau et al. 2007, Beesley et al. 2008). The timing of natural patch dynamics could have coincided with a decline in pH. Indeed, the changes could have resulted from other abiotic factors, such as increased temperature (Reichert and Buchholz 2006), or equally from biological factors, such as changes in predator abundance (Enderlein and Wahl 2004, Nav-arrete and Manzur 2008). Sea surface temperature appears to have increased slightly over the observation period (Wootton et al. 2008: Fig. S1) but there are no
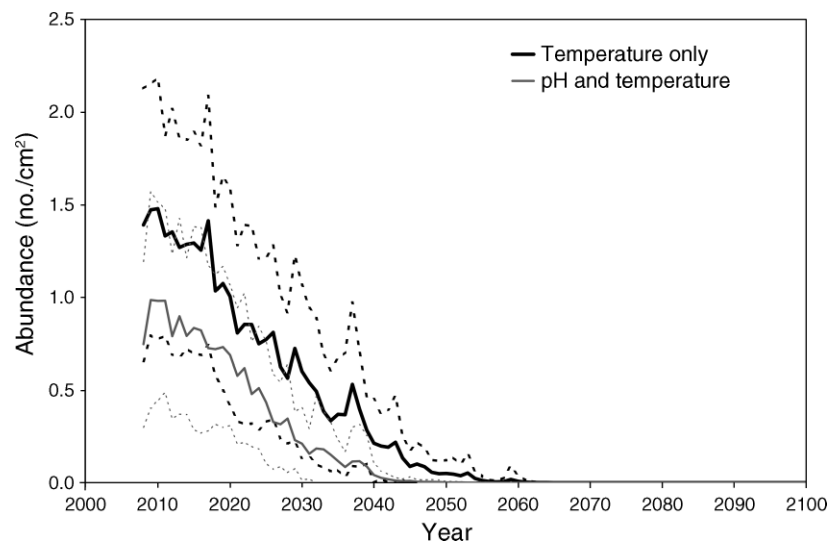

Fig. 6. Mean of 100 model runs of acorn barnacle population abundance from 2008 to 2020 with temperature-only forcing and temperature and pH forcing. Dashed lines indicate ±SD (black for temperature-only forcing; gray for pH and temperature forcing).
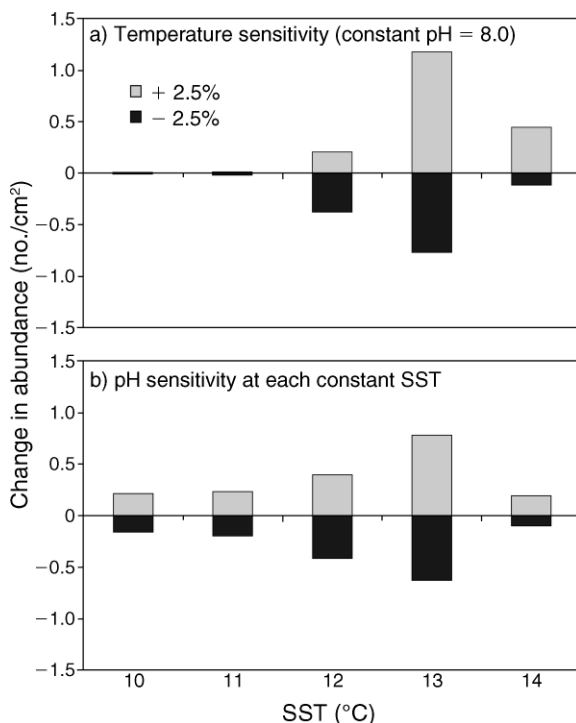
FIG. 7. Sensitivity of the acorn barnacle population abundance model to a 2.5% increase and 2.5% decrease in (a) sea surface temperature (SST; with constant pH 8.0) and (b) pH (at each constant temperature) after the model has equilibrated to pH 8.0 and each of the temperatures (10–14°C).

records for abundance of mobile predators. The Wootton et al. (2008) study is an important analysis of community dynamics, demonstrating that individuals or populations may not respond to environmental change in a straightforward shift, which this present modeling study suggests. Community interactions may buffer the local environment and actually provide some additional level of resilience to calcifying organisms.

As emphasized by Poloczanska et al. (2008), changes in population abundance of competing species can significantly impact the abundance of their competitors and their predators. Chthamalus species have yet to be examined in response to elevated CO$_2$, although the disappearance of S. balanoides will create free space for Chthamalus and other species. Elminius modestus, for example, appears to tolerate elevated CO$_2$ at similar SST to those described here, showing only subtle impacts on growth rate but no impact on survival or shell development (Findlay et al. 2009b). Elminius modestus is a spatial competitor to S. balanoides and may therefore benefit to some extent from future changes in temperature and ocean chemistry where distributions overlap. Few climate change and ocean acidification experiments have been carried out on algae, although longer term studies on sea grass showed a potential increase in photosynthesis and productivity in lowered pH conditions (Palacios and Zimmerman 2007), hence

macro-algae may not be detrimentally impacted by ocean acidification (Beer and Koch 1996), which will additionally modify community responses to future environmental changes.

Our simulations are for populations at the southern edge of their distribution, and it is possible that different consequences of ocean acidification and warming may be found at mid or northern locations within S. balanoides range, particularly as the frequency with which stressful events occur will vary across latitudes and hence the interaction between environmental factors will also change. Although the model presented in this study is a simple representation of one species' population abundance, it is a first link between experimental data on individuals and predicting population effects. Future modeling studies could become more detailed, including other species or investigating differences between habitats on a local scale, but should be parameterized by empirical data.

Two assumptions made in this model study warrant some discussion. First, the inclusion of a gregarious term: Poloczanska et al. (2008) tested several models against data from the UK south coast, two of which were used to determine whether a gregarious term should be included. The model–data fit was much closer when the gregarious function was included. Semibalanus balanoides is a species that is known to settle where conspecifics are located and hence this function should be incorporated into the model. This represents an open population where the recruits are specific about their settlement area. Furthermore, the gregariousness function arguably also captures stock size effects. Without S. balanoides contributing to the larval pool over a certain region, the larval supply to an "open" population would decline to nothing. When there is no gregariousness included (G = 1), the model fit to data is worse (Appendix D). The population dies out roughly 20 years later than in the model with gregariousness, and the population dies out more quickly when pH and SST forcing is used than when there is SST-only forcing (year 2077 and year 2098, respectively). The second assumption is that of linear trend of increasing SST and decreasing pH. The linear trends are simplified models to allow a first estimation of the relative influences of pH and SST on a population. The current projections for future SST and pH as determined by ocean–atmosphere general circulation models (OAGCM) are not linear, they are accelerating (Orr et al. 2005, IPCC 2007). This would bring forward the timing of population collapse in this model, and hence our linear trends are conservative estimations. Furthermore, these OAGCM projections provide information about the global mean trends, but do not provide information about regional trends, which this study uses. Further research should assess the impacts of different climate scenario projections (e.g., IPCC 2007 scenarios or United Kingdom Climate Predictions 2009 [UKCP09] scenarios) on local populations.

The outcomes of our models are only valid if we make the assumption that no adaptation or acclimation to a changing environment takes place in these organisms. It seems unlikely that, at the southern edge of their geographic range, *S. balanoides* will be able to tolerate increasing temperatures (range shifts); however, in mid and northern parts of the range, where pH has potentially more impact than SST, acclimation or adaptation may be possible. Transplant field experiments showed that local adaptation in thermal tolerance can occur across small spatial scales (Bertness and Gaines 1993). There is also evidence of organisms adapting to lowered pH conditions by either changing their shell mineral content (e.g., cold-water corals living close to the aragonite saturation horizon in the Pacific Ocean; Guinotte et al. 2006) or by forming protective outer membranes (e.g., mussels found on the edge of hydrothermal vents; Tunnicliffe et al. 2009), which hints at mechanisms that may help counteract some of the impacts of ocean acidification.

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APPENDIX A

Nauplii experimental methods (*Ecological Archives* E091-206-A1).

APPENDIX B

Model parameters and equations (*Ecological Archives* E091-206-A2).

APPENDIX C

Model formation for pH and data collection (*Ecological Archives* E091-206-A3).

APPENDIX D

Model statistical and sensitivity analyses (*Ecological Archives* E091-206-A4).